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Multiple phenological responses to climate change among 42 plant species in Xi'an, China

Junhu Dai · Huanjiong Wang · Quansheng Ge

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Abstract Phenological data of 42 woody plants in a temperate deciduous forest from the Chinese Phenological Observation Network (CPON) and the corresponding meteorological data from 1963 to 2011 in Xi'an, Shaanxi Province, China were collected and analyzed. The first leaf date (FLD), leaf coloring date (LCD) and first flower date (FFD) are revealed as strong biological signals of climatic change. The FLD, LCD and FFD of most species are sensitive to average temperature during a certain period before phenophase onset. Regional precipitation also has a significant impact on phenophases of about half of the species investigated. Affected by climate change, the FLD and FFD of these species have advanced by 5.54 days and 10.20 days on average during 2003–2011 compared with the period 1963–1996, respectively. Meanwhile, the LCD has delayed by 10.59 days, and growing season length has extended 16.13 days. Diverse responses of phenology commonly exist among different species and functional groups during the study period. Especially for FFD, the deviations between the above two periods ranged from −20.68 to −2.79 days; biotic pollination species showed a significantly greater advance than abiotic pollination species. These results were conducive to the understanding of possible changes in both the structure of plant communities and interspecific relationships in the context of climate change.

J. Dai \cdot H. Wang \cdot Q. Ge (\boxtimes) Institute of Geographical Sciences and Natural Resources

Research, Chinese Academy of Sciences, A 11, Datun Road, Chaoyang District, Beijing 100101, People's Republic of China e-mail: geqs@igsnrr.ac.cn

H. Wang University of Chinese Academy of Sciences, 19A Yuquan Road, Beijing 100049, People's Republic of China

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Introduction

Numerous studies have suggested that global changes have affected terrestrial ecosystems (IPCC [2001\)](#page-9-0). The response of phenology to warming across the northern hemisphere seems to be especially well documented (Root et al. [2003;](#page-9-0) Parmesan and Yohe [2003;](#page-9-0) Parmesan [2007\)](#page-9-0). Phenology is a sensitive, easily observable, and integrated indicator of climate change, and it also has various ecological implications (Zhang et al. [2004\)](#page-9-0). Phenological changes can affect the cold hardiness of species (Hänninen [1991\)](#page-9-0), the distribution (Chuine and Beaubien [2001](#page-8-0)) and productivity (Loustau et al. [2005](#page-9-0)) of tree species. At the ecosystem scale, phenology factors, especially growing season length, may influence energy and moisture exchange, seasonal carbon cycle and aerosol formation between land surface and atmosphere (Chen and Xu [2012](#page-8-0)). Therefore, studying the direction and magnitude of phenological changes may help us understand the interaction between vegetation dynamics and climate.

Many studies have shown significant advances of phenological events in spring whereas changes of timing of events in autumn are uncertain (Menzel [2000;](#page-9-0) Cayan et al. [2001;](#page-8-0) Gordo and Sanz [2010;](#page-9-0) Ge et al. [2011](#page-9-0)). Some of these studies showed regional variation in phenological changes based on observation of a single or a small set of species (Schwartz and Reiter [2000](#page-9-0); Emberlin et al. [2002;](#page-8-0) Matsumoto et al. [2003](#page-9-0); Du et al. [2010](#page-8-0)). Other studies also focus on phenological responses among numerous species (Menzel et al. [2006](#page-9-0); Bai et al. [2010](#page-8-0); Wolkovich et al. [2012](#page-9-0)). For instance, Abu-Asab et al. ([2001](#page-8-0)) reported that 89 of 100 species examined in the Washington DC area bloomed earlier during a 30-year period, and that the change was more significant in early-flowering species than in late-flowering species. Fitter and Fitter ([2002\)](#page-9-0) found that 24 % of 385 species at a single location in south-central England showed later flowering in contrast with other species. Such asynchronous responses to environmental changes among species may lead to shifted community structure or ecosystem processes. For example, Mckane et al. ([1990\)](#page-9-0) showed that the advances of activity in biological processes (flowering, leaf expansion, root growth, nutrient uptake, etc.) altered the competitive interactions among species. Cleland et al. [\(2006](#page-8-0)) found that elevated $CO₂$ accelerated flowering of forbs but delayed it for grasses. These phenological responses lead to decreased phenological complementarity, which means increased temporal overlap in flowering timing and increased resource competition among species (Cleland et al. [2006\)](#page-8-0). Thus it is important that asynchronous responses among species can be observed and investigated in order to understand the effects of climate change on community structure and ecological processes. However, researchers seldom monitor the phenology of all species in a community, limiting research progress at the community scale (Cleland et al. [2007](#page-8-0)).

Aiming to lay the foundation for further research of community-scale phenology and the management of regional ecosystems, we chose Xi'an, Shaanxi Province, China one of the stations of Chinese Phenological Observation Network (CPON) with the most abundant historical data as our study area. We focused on the relationship between climatic factors (temperature and precipitation) and three phenophases, including first leaf dates (FLD), leaf coloring date (LCD), as well as first flowering date (FFD) among 42 woody plant species within a typical temperate forest community from 1963 to 2011. Next, we identified the direction and magnitude of phenological changes in each species that were triggered mainly by climate change. In order to determine whether the biological characteristics affect variations in phenophases and their changes, we divided these species into two functional groups according to life form—a key characteristic reflecting plant function and adaptation to the environment. Then we compared the phenophases (FLD, LCD and FFD) and their changes between different life form groups. A particularly strong relationship between reproductive phenology traits (represented by FFD in this study) and pollination success was expected (Parra-Tabla and Vargas [2007\)](#page-9-0). So we also compared FFD and its changes between different pollination types. Overall, our objectives were to: (1) quantify species' phenological responsiveness to climate variables; (2) assess phenological changes on the community level in a typical temperate deciduous forest; and (3) identify the distinctions between the phenological responsiveness in different functional groups.

Materials and methods

Study site

Xi'an, located in the Wei River Plain at north-central China (34°12′N, 108°57′E , 440 m a.s.l.), has a typical temperate continental monsoon climate with mean annual temperature of 13.7 °C (Bai et al. [2010\)](#page-8-0). The yearly maximum and minimum temperature are 26.3 °C in July and −0.5 °C in January, respectively. The area has an annual mean precipitation of 573.1 mm, and receives most of it (78 %) during summer and autumn (May–October). The major zonal vegetation type in this site is deciduous broad-leaved forest. The objective species are woody plants, belonging to the north China flora (Lei [1999\)](#page-9-0).

Phenological and meteorological data

All phenological data for this study are from CPON, which was established in 1963. Since that time, CPON has been administrated through the sponsorship of the Institute of Geographic Sciences and Natural Resources Research (IGSNRR) at Chinese Academy of Sciences. There were two discontinuities of the observations for each site. From 1969 to 1972, the observation was affected by the social disorders of the Cultural Revolution. And during the period 1997–2002, observations were interrupted due to the lack of sponsorship funds. So data for this study are available only for the periods 1963–1968, 1973–1996, and 2003–2011. In addition, there are a few missing data in certain years due to discontinuous observations (Table [1\)](#page-2-0).

The FLD, LCD, and FFD of 42 species were studied, with 6 species having no FFD data (Table [1\)](#page-2-0). Observations of each phenophase conform to uniform observation criteria and guidelines (Wan and Liu [1979](#page-9-0)). Based on these criteria, the FLD and FFD are defined as the date when a fixed individual formed the first full leaf and the first full flower, respectively. And LCD was defined as the date when the individual shows yellow leaves over 90 % of their crowns. The period between FLD and LCD can be regarded as the photosynthesis period of the plant, and therefore its length is calculated as the growing season length (GSL) (Menzel [2003\)](#page-9-0). All 42 species are woody plants, belonging to 26 families (Table [1](#page-2-0)). With the exception of 3 exotic species, the other 39 native species are dominant species inside a typical deciduous broadleaved community (Table [1](#page-2-0)). The phenological data were collected in the Xi'an Botanical Garden, located about 10 km away from the city center.

The data of daily climate factors, including mean temperatures and precipitation in Xi'an were obtained from the China Meteorological Data Sharing Service System. These data are well checked and normalized by China Meteorological Administration before being issued (<http://cdc.cma.gov.cn/>).

of first leaf dates, MLCD mean timing of leaf coloring date, MFFD mean timing of first flowering date (all from 1963 to 2011). LF Life form, PT pollination type

^a Exotic species

 C T Tree species, S shrub species

 d_A Abiotic pollination, B biotic pollination

^b No data

Methods

Analysis of relationship between phenology and climate factors

The timing of phenological events was probably impacted by climate factors during a certain period before its occurrence (Matsumoto et al. [2003](#page-9-0)), and this can be used to estimate the optimum period (OP) during which a certain climate factor affects phenological events most markedly. In this method, OP is defined as:

$$
OP = [BP, EP] \tag{1}
$$

where EP is the end date of OP (day of year, DOY), and is defined as the average date of the phenophase from 1963 to 2011. BP is the beginning date of the period (DOY). Then the Pearson's correlation coefficient (R) between the phenophase (FLD, LCD or FFD) and climate factor (precipitation or the average temperature) during [BP, EP] was calculated by moving each BP from 1 January to EP−1 by a step length of 1 day. The period [BP, EP] with the highest |R| was regarded as OP during which climate factors affected phenological events most markedly. Meanwhile, the significance of the correlation coefficients were tested by using 2-tailed t-tests. The slopes of regression between the annual timing of phenological event (FLD, LCD or FFD) and the climate variable (precipitation or the average temperature) during the corresponding OP were used as a measure for the temperature sensitivity or precipitation sensitivity of each phenophase.

Phenological changes in the community

Based on our previous study (Bai et al. [2010\)](#page-8-0), abrupt changes of temperature occurred in 1995 in Xi'an. In view of this result and the observation years, we selected 1963–1996 and 2003– 2011 as two contrasting periods. By preliminary analysis, we found the mean annual temperature during 2003–2011 to be significantly warmer than that during 1963–1996 in Xi'an (15.1 °C vs 13.4 °C, unequal variance *t*-test, $P < 0.001$). The mean annual precipitation of the latter period (592.9 mm) is more than that during 1963–1996 (563.6 mm), but the difference is not significant ($P=0.57$). Therefore, choosing these two periods is appropriate for analyzing the phenological responses to climatic change, especially temperature change. The mean FLD, LCD, GSL and FFD of all the species during each period were calculated. A boxplot method was used to depict phenological differences at the community level between the two studied periods.

In addition, for each species, the deviation in FLD, LCD, GSL and FFD between the above two periods was calculated. An unequal variance *t*-test was performed to test whether the deviations differed significantly from zero.

Change of phenology in different groups

To identify connections between the biological characteristics of plants and the distinct responses of plant phenology, we used an approach similar to that of Fitter and Fitter [\(2002](#page-9-0)) to divide the species into different plant functional groups.

First, we divided the 42 species into two groups, i.e., tree species and shrub species according to their life forms (Table [1\)](#page-2-0). Our definition of a tree is a perennial woody plant with a single main stem or trunk and a minimum height of 6 m at maturity (Mitchell [1974](#page-9-0); Huxley and Griffiths [1999\)](#page-9-0). A shrub or bush is distinguished from a tree by its multiple stems and shorter height, usually less than 6 m tall.

Secondly, we differentiate abiotic pollination species from biotic pollination species in compliance with pollination types. Abiotic pollination is mediated without the assistance of other organisms (Mori et al. [2009\)](#page-9-0), while the more common biotic pollination requires biotic pollinators, i.e., organisms that carry pollen grains from the anther to the receptive part of the carpel or pistil (Mori et al. [2009\)](#page-9-0). In this study, abiotic pollination refers to pollination by wind, while biotic pollination means pollination by insects. We identified the pollination types of each species by field observations and survey (Table [1](#page-2-0)).

We then compared differences in phenophases (FLD, LCD and FFD) and their deviations in the period 2003–2011 from the mean over the period 1963–1996 between groups of tree species and shrub species. In particular, FFD and its deviations between abiotic pollination species and biotic pollination species were also checked using unequal variance t-test.

Results

Relationship between phenophases and climate variables

Figure [1](#page-4-0) shows the OP of 42 species during which temperature or precipitation affected each phenophases most strongly. Generally, the length of OP for FLD and FFD (correlated with temperature or precipitation) ranged from 19 to 100 days (mean 36 days) and 13 to 194 days (mean 56 days), respectively (Fig. [1\)](#page-4-0). The length of OP for LCD was between 25 and 244 days (100 days on average). Hereafter, we define the average temperature during OP of each phenophase as 'OP temperature', and define the total precipitation during OP of each phenophase as 'OP precipitation'.

Analysis of correlation shows that phenology has a clear reaction to temperature changes (Fig. [2a](#page-4-0)). The correlation coefficients of all the 42 species between FLD and OP temperature were negative and 95.2 % of them (40 species) achieved the significant level of $P<$ 0.05. The mean correlation coefficients between FLD and

Fig. 1 The optimum period (OP, black bars) of 42 species during which temperature or precipitation affected each phenophase most markedly. T Temperature, P precipitation. Species numbers are defined in Table [1](#page-2-0)

OP temperature was -0.73 ± 0.13 (mean \pm SD). For LCD, 95.2 % of the correlation coefficients (40) against OP temperature were positive, and 66.7 % of them achieved the significant level of $P < 0.05$. The average correlation coefficient of LCD against OP temperature was $0.47\pm$ 0.28 (mean \pm SD). With regard to FFD, all 36 correlation coefficients against OP temperature were significant $(P<0.05)$, with a mean of -0.81.

Fig. 2a,b Responses of first leaf date (FLD), leaf coloring date (LCD), as well as first flowering date (FFD) of 42 species to OP temperature. a Pearson's correlation coefficients of FLD, LCD and FFD against corresponding OP temperature. b Regression slopes of FLD, LCD and FFD against corresponding OP temperature

The slope of linear regression between phenophases and OP temperature is considered a measure of temperature sensitivity (Fig.[2b\)](#page-4-0). The responses of FLD and FFD showed a good consistency: they advanced by 1.47–5.48 days[°]C⁻¹ and 2.84–11.44 days°C−¹ , respectively (Fig. [2b\)](#page-4-0). However, the responses of LCD seem more complex and dispersive: two species advanced by 4.43—6.95 days°C⁻¹, and the others delayed by 2.10–13.64 days°C−¹ (Fig. [2b\)](#page-4-0). Overall, mean temperature sensibility of the FLD (-2.93 days^{°C $^{-1}$}), the LCD (5.99 days°C⁻¹), and FFD (−4.34 days°C⁻¹) differed significantly from each other. In addition, analysis of variance followed by two-sample F-test showed that the variance of the temperature sensitivities for FLD and FFD was significantly less than that of LCD $(P<0.001)$.

Furthermore, the correlation coefficients between the temperature sensitivities and mean onset dates of FLD was positive (Pearson's $R=0.51$, $P<0.001$). However, the temperature sensitivities of FFD correlate negatively with their mean onset dates (Pearson's $R=-0.65$, P< 0.001). The temperature sensitivities of LCD were barely related to their mean onset dates (Pearson's $R=0.05$, $P=0.66$).

The relationships between phenophases and OP precipitation were complex, and varied substantially among species (Fig. 3). The correlation coefficients of FLD of 34 species (80.1 %) against OP precipitation were positive (23 of them were significant) with a mean of 0.43, whereas correlation coefficients of FLD of the other 8 species was negative (none was significant) with a mean of −0.18. Similar to FLD, FFD of 30 species (83.3 %) correlated positively with OP precipitation (19 of them were significant) with the mean correlation

754 Int J Biometeorol (2013) 57:749–758

coefficients of 0.42 and FFD of 6 species (16.7 %) correlated negatively with OP precipitation (2 of them were significant) with the mean correlation coefficients of −0.24. Regarding LCD, few species correlated significantly with OP precipitation: only 7 species showed a significant negative correlation and only 1 species showed significant positive correlation.

The slope of linear regression between phenophases and OP precipitation is shown in Fig. 3b. The FLD of 34 species delay by $0.04-0.27$ daysmm⁻¹ while 8 species advanced 0.03–0.13 daysmm^{-1} (Fig. 3b). The FFD of 30 species delay by $0.04-0.27$ daysmm⁻¹ while 6 species advanced 0.09–0.55 daysmm⁻¹ (Fig. 3b). And the precipitation sensibility of LCD was -0.13 to 0.12 daysmm⁻¹. Overall, when the OP precipitation increased by 1 mm, the FLD and FFD would delay −0.10 days and −0.08 days on average, respectively. The mean precipitation sensitivity of LCD was relatively weak (only -0.01 daysmm⁻¹).

Phenological change between 2003–2011 and 1963–1996

The boxplot of each phenophase of 42 species in 1963– 1996 and 2003–2011 shown in Fig. [4](#page-6-0) illustrate the differences in community phenology between these two periods. The median of FLD and FFD was 5.27 days and 10.88 days earlier in 2003–2011 than in 1963–1996, respectively. On the other hand, the median of LCD was 10.09 days later in 2003–2011 than in 1963–1996. The interquartile ranges for FLD and LCD in 2003–2011 was 5.79 and 3.42 days greater than those in 1963–1996, respectively. However, the interquartile range for FFD in the latter period was 3.96 days less than the range in 1963–1996..

Fig. 3 Responses of the FLD, LCD and FFD of 42 species to OP precipitation. a Pearson's correlation coefficients of FLD, LCD and FFD against corresponding OP precipitation. b Regression slopes of FLD, LCD and FFD against corresponding OP precipitation

Fig. 4 Boxplot of mean FLD, LCD and FFD of 42 species in the community in 1963–1996 and 2003–2011

The observed changes for FLD, LCD, GSL and FFD between 2003–2011 and 1963–1996 are summarized in Fig. 5. All the species showed negative deviations in FLD, with 29 species (69.0 %) being significantly advanced (P < 0.05). With regard to LCD, 2 species (4.8 %) advanced (one species achieved the significance level of 0.05); while other 40 species (95.2 %) were delayed (25 species achieved the significance level of 0.05). The GSL of all the species was extended (33 species achieved the significant level of 0.05). The overall mean advance of FLD was −5.54±2.47 (mean± SD) days and the mean delay of LCD was 10.59 ± 6.76 (mean±SD) days, which leads to an extension of GSL by 16.13 ± 7.21 (mean \pm SD) days. The FFD of the entire 36 species advanced by -10.20 ± 3.74 (mean \pm SD) days. Among them, FFD deviations of 33 species (91.7 %) were significant.

Between-group contrasts of phenological deviations

The between-group contrasts of mean phenophases from 1963 to 2011 and deviations in phenophases in the period 2003–2011 from the mean over the period 1963–1996 are presented in Table [2.](#page-7-0) Tree species had later FLD and FFD than shrubs, but tree advances were stronger than those of shrubs. Conversely, the tree species had a later LCD than shrub species, but the delay of LCD for tree species was weaker than for shrub species. None of these differences between tree species and shrub species achieved a significance level of 0.05 (Table [2](#page-7-0)). With respect to pollination type, we found that flowering phenology had a strong interaction with pollination mechanism. The abiotic pollination

Fig. 5a–d Frequency distributions of the deviations in phenophases in the period 2003–2011 from the mean over the period 1963–1996. Categories are 3-day periods. Solid shading of columns represent

species for which the deviation was significantly $(P<0.05)$ different from zero. a First leaf dates; b leaf coloring dates; c growing season length; d first flowering date

Table 2 Comparisons of mean phenophases and their deviation between groups classified by different functional types. Mean FLD, LCD, and FFD mean phenophase (day of the year, DOY) from 1963–2011; FLD, LCD, and FFD deviation deviations of FLD, LCD and FFD in the period 2003–2011 from the mean over the period 1963–1996, respectively, N the numbers of the samples, Mean average values, SD standard deviation, Probability probability to accept the null hypothesis (the mean value of the two groups was equal) by unequal variance *t*-test

species flowered significantly earlier than biotic pollination species (Table 2). Moreover, biotic pollination species showed a significantly greater advance than abiotic pollination species (−10.98 days vs −6.96 days, $P<0.05$).

Discussion and conclusions

Our study confirms that phenology is a sensitive indicator of temperature change (Root et al. [2003](#page-9-0); Badeck et al. [2004](#page-8-0); Körner and Basler [2010](#page-9-0)). The phenological timings of most species (95.2 % for FLD, 100 % for FFD and 69.0 % for LCD) correlated significantly with corresponding OP temperature, with the mean correlation coefficient being −0.73, 0.47 and −0.81, respectively. The sensitivity of FLD, LCD, and FFD to OP temperature varies among species: −5.48 to −1.47 (−2.93 on average) days per °C for FLD, −6.95 to 13.64 (5.99 on average) days per °C for LCD, and −11.44 to −2.84 (−4.34 on average) days per °C for FFD. Therefore higher temperature would lead to earlier leaf unfolding and flowering timing, and an overall later leaf coloring timing. Furthermore, the variance in temperature sensitivity of LCD is much greater than that of FLD. A possible explanation is that LCD in autumn tends to be more difficult to define and observe, and is subject to sudden individual weather events such as a single frost or high winds (Sparks and Menzel [2002\)](#page-9-0). We also noted that species with an earlier leaf unfolding time were more sensitive to OP temperature—a finding similar to that of Menzel et al. ([2006\)](#page-9-0). In contrast, species with earlier FFD were less sensitive to OP temperature. These findings imply that flower phenology may be affected by other environmental factors. For example, photoperiod has been known to regulate flowering time in many plant species (Jeong and Clark [2005\)](#page-9-0). Further experimental work on the impact of the interaction of photoperiod and temperature on phenophases is required.

Apart from temperature factors, we also found that precipitation has a potential impact on phenophases of some species within deciduous forests. The FLD and FFD of many species (54.8 % for FLD, 52.8 % for FFD) correlated significantly and positively with corresponding OP precipitation. Towards LCD, only 7 species showed significantly negative correlation with OP precipitation. We highlight two possible causes for these results. First, for most of species, precipitation has an indirect effect on phenology by causing the temperature to decrease. Through our analyses, the OP temperature of many species (52.4 % for FLD, 75 % for FFD, 33.3 % for LCD) correlated significantly and negatively with OP precipitation (not shown). Typically, high rainfall increased cloud cover, resulting in colder daytimes. The FLD and FFD would then delay in response to cooling temperature. Second, precipitation may have direct effect on the phenology of several species. For 7 species (16.7 %), the partial correlation coefficients between FLD and OP precipitation with the effect of OP temperature removed were significantly positive (not shown). This result indicated that precipitation can directly influence phenological timing of some specific species other than simply by making the temperature change. Human activity in particular may partially affect this direct effect in our study, because the gardener would irrigate the plants in the Xi'an botanical garden in extreme drought conditions. Above all, precipitation may play a crucial role in the phenological timing of some specific species, but the link between water relations

and plant growth in woody plants is complex and need further investigation.

The observed phenology of plant species in Xi'an had changed notably in recent decades. All 42 species began the growing season earlier (69 % significantly), 95.2 % of them ended the growing season later (59.5 % significantly), and 100 % of them extended the growing season length (78.6 % significantly) in 2003–2011 compared with 1963–1996. For the reproductive phenology, the FFD of all the species was also earlier (91.7 % significantly) in the latter period. The mean deviations of FLD, LCD, GSL and FFD were −5.54, 10.59, 16.13 and −10.20 days during 2003–2011 compared with 1963–1996, respectively. In addition, the statistical dispersion of community phenology was also changed, e.g., the interquartile range of FLD and LCD increased but that of FFD decreased. These recent rapid shifts in phenology coincide well with the notable climate change, especially temperature change, in the study area. Because it was 1.7 °C warmer in the period 2003–2011 than in 1963–1996, the difference in precipitation between these two periods is not statistically significant. In view of the recent rapid urbanization of Xi'an, an urban heat island effect (HIE) may contribute to local climate change. Previous study has shown that the urbanization effect accounted for 20 % of warming trends in China (Wang and Ge [2012\)](#page-9-0). In Xi'an, the urban area was 0.485 °C warmer than rural areas on average in recent years (Liu and Yin [2008](#page-9-0)). Hence, HIE may account for about 28 % of climate change (the overall warming of 1.7 °C) and phenological change in Xi'an, but the actual climate change beyond HIE was still very dramatic and could not be ignored.

We found species within the community to be remarkably diverse in their phenological reactions. For example, the largest deviation of FFD in the period 2003–2011 from the mean over the period 1963–1996 was −20.8 days, while the minimum was only −2.79 days. These phenological changes of certain species are key to their success in reproduction and coexistence with others. Our results may be helpful for decision-making in regional ecosystem management and conservation, e.g., by selecting proper plant species whose phenophases have less temporal overlap with others to minimize interspecific competition when implementing afforestation projects.

The distinct responses to climate change among species and between different functional groups will disrupt communities, altering competitive and other interactions (Fitter and Fitter [2002\)](#page-9-0). In our study area, if 42 species are sorted according to first leaf timing in 1963–1996 and in 2003– 2011, the average change in rank between the two lists is 2.76, with 4 species exhibiting rank changes of more than seven places. As far as different plant functional groups were concerned, although the life form could explain the difference of phenological change to a small degree, the difference of FFD deviations between two pollination types

was significant: the advance of FFD of biotic pollination species was significantly greater than that of abiotic pollination species. Taking into consideration the fact that the biotic pollination species flower later than abiotic pollination species, these discrepant FFD changes may lead to increasing temporal overlap, and thus, intensify competition for one or more resources between the two pollination groups. Therefore, these multiple phenological changes, together with other consequences of climate change, such as shifts in species distribution (Chuine 2010), may alter the interactions and dynamics of populations and have profound impacts on the ecosystem and evolutionary consequences (Peñuelas and Filella [2001](#page-9-0); Devaux and Lande 2010; Haggerty and Galloway [2011](#page-9-0)). Future studies should investigate how these multiple phenological responses to climate change affect interactions among species and their ability to persist in changing climate.

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